

## Relative Dental Development of Upper Pleistocene Hominids Compared to Human Population Variation

ROBERT L. TOMPKINS

*Department of Anthropology, University of New Mexico, Albuquerque,  
New Mexico 87131*

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**ABSTRACT** The relative development of permanent teeth in samples of Neandertal/archaic *Homo* and Early Modern/Upper Paleolithic hominids is compared to the range of variability found in three recent human samples. Both fossil hominid samples are advanced in relative M2 and M3 development compared to white French-Canadians, but only the Neandertal/archaic *Homo* M3 sample is advanced when compared to black southern Africans. Both fossil hominid samples are delayed in relative I1 and P3 development compared to the recent human samples. Two hypotheses concerning the significance of the advanced M3 and M2 development found in both hominid groups and southern Africans compared to French-Canadians are discussed. The first postulates that the differences in relative molar development are due simply to variation in tooth/jaw size relationships. The second postulates that the relatively advanced M3 and M2 development found in the fossil hominids and southern Africans is a correlate of their potential for advanced skeletal maturation compared to French-Canadians and other European-derived populations. It appears that dental development patterns have continued to evolve from the Upper Pleistocene to present times, and that Neandertals and Early Moderns shared similar patterns of relative dental development.

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The study of differences in developmental rates and patterns between living humans and their fossil ancestors has a long history in paleoanthropology (Buxton, 1928; DeBeer, 1948; Keith, 1931; Mann, 1968, 1975; McCown and Keith, 1939; Vallois, 1937, 1961; Weidenreich, 1941, 1951). Recent years have seen much debate over the rate and patterning of ontogeny in Plio-Pleistocene hominids (Beynon and Dean, 1987, 1988; Beynon and Wood, 1987; Bromage, 1987; Bromage and Dean, 1985; Conroy and Vannier, 1987, 1991; Dean, 1987a,b; Dean and Beynon, 1989; Dean et al., 1993a; Mann, 1988; Mann et al., 1987, 1990, 1991a,b; Simpson et al., 1990, 1991, 1992; Smith, 1986, 1987, 1989, 1991). At the same time, there has been renewed interest in the evolution of hominid growth and development in

the Upper Pleistocene (Dean et al., 1986; Minugh-Purvis, 1988; Stringer et al., 1990; Trinkaus and Tompkins, 1990).

While several studies concerning growth and development have been conducted on Upper Pleistocene hominid remains, especially Neandertals, most of these have focused on differences from modern humans of equivalent maturity level or estimated age in anatomical proportions (relative and absolute), shape and robusticity (Buxton, 1928; Ferembach et al., 1970; Fraipont, 1936; Heim, 1982; Martin 1926; Petit-Maire-Heinz, 1958; Weinert, 1925), and/or the relative timing in ontogeny of the appearance of

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adult morphological features (Tillier, 1982, 1983, 1984, 1986, 1989; Tompkins and Trinkaus, 1987; Trinkaus, 1986; Vlcek, 1964, 1967, 1970). Few studies have dealt with the rates and/or patterning of growth and development in Upper Pleistocene hominids.

The study by Dean et al. (1986) on the Devil's Tower (Gibraltar 2) child, using a combination of perikymata counts and radiographic analysis of developing teeth, suggested that the postnatal rates of dental maturation in this Neandertal were somewhat accelerated with respect to modern humans. Specifically they noted more advanced calcification of the mandibular second premolars, second permanent molars, and first and second incisors than expected for modern humans, although this Neandertal's overall dental development is within modern human ranges. Dean et al. state that this somewhat advanced dental development "... might suggest a slight increase in the rate of general growth and development in this specimen ..." compared to modern humans (Dean et al., 1986, p. 307).

Legoux (1965, 1966, 1970), while attempting to provide age estimates for various immature Neandertals, suggested that they had different patterns of tooth development than modern humans. While there was variability between the specimens, some of the fossils seemed to have precocious development of their anterior teeth. Skinner (1978) found some differences in relative dental development between Neandertals and recent humans, but these differences were far less than those between non-human primates and Neandertals. Wolpoff (1979), using a modified Miles (1963) technique of dental wear aging, suggested that the third molars of the Krapina Neandertals erupted closer to 15 years instead of the 20 years common for Euroamericans.

The present study compares relative dental development in Neandertals and other archaic *Homo* specimens and Early Modern/Upper Paleolithic specimens to three samples of recent humans: black southern Africans, white French-Canadians, and prehistoric Native Americans. In comparisons of relative dental development, the degree of formation of various teeth is compared between individuals who have a specific "reference tooth" at the same stage of develop-

ment. Comparisons of the three recent human samples have been presented in a previous paper (Tompkins, 1996). The purpose of the present study is to determine whether Neandertal and Early Modern hominid subadults deviate significantly from the range of variability found among the three recent human samples, and to interpret the significance of the presence or lack of any differences in the fossil hominids with respect to the evolution of modern human patterns of ontogeny.

## MATERIALS

The French-Canadian sample utilized for this study consists of 850 radiographs from 329 individuals drawn from Dr. A. Demirian's mixed longitudinal collection of dental radiographs housed at the Université de Montréal. Of these 850 radiographs, 468 were of males and 382 were of females. The black southern African sample was gathered from radiographs housed at the Dental School of the University of the Witwatersrand in Johannesburg, South Africa, the Medical University of South Africa (MEDUNSA), and from radiographs of Botswanan children taken by Mike Barter of the University of the Witwatersrand (courtesy of the Ministry of Health, Botswana). A total of 691 radiographs from 687 individuals (333 males and 354 females) were utilized for this sample. The Native American sample consists of radiographs taken by the author on prehistoric Native American subadults from skeletal collections curated by the Maxwell Museum of Anthropology of the University of New Mexico, the University of Kentucky (Lexington), and the Hearst Museum of the University of California, Berkeley. The total number of radiographs in this collection is 520. These three recent human samples are described in greater detail in Tompkins (1991, 1996).

The Early Modern/Upper Paleolithic sample comprises 57 children from sites in western and eastern Europe, the former Soviet Union, and the Middle East, with the bulk of the sample deriving from archaeological levels not earlier than the Aurignacian (beginning approximately 31–34 kya BP) and as late as approximately 11 kya BP. However, two specimens from the site of Qafzeh in Israel (4 and 11) date by thermolumines-

cence to 92 kya BP (Valladas et al., 1988) and by ESR to 115 kya BP (Schwarcz et al., 1988). Also included is the Skhul I specimen which may date to around 90 kya BP (Stringer et al., 1989). These specimens are included in the Early Modern sample based on their morphological affinities with other Early Modern specimens, rather than being included with the Neandertal/archaic *Homo* sample based on chronology. While some may take issue with this approach, it is the taxonomic/grade assignment employed by many workers (Tillier, 1989; Trinkaus, 1983; Vandermeersch, 1981).

The Neandertal/archaic *Homo* sample is composed of 29 individuals ranging in geological age from the last interglacial (Deep Sea isotope state 5e) to "classic" Neandertal sites from Wurm II times (isotope stage 3). The sample includes 27 specimens considered Neandertal in the strict sense of the term, and two non-Neandertal specimens from Morocco, Jebel Irhoud 3 and Rabat 1. Jebel Irhoud 3 derives from an archaeological level characterized as Levallois Mousterian (Hublin and Tillier, 1981). The Rabat 1 specimen was discovered in a quarry stone derived from a consolidated dune which has been given a Riss/Wurm age based on invertebrate marine fauna found within it (Minugh-Purvis, 1988).

Dental radiographs for many of the fossil specimens were made available to me by Mark Skinner. Those specimens for which radiographs were not available were either X-rayed by me using a Lumix 70-II dental X-ray machine, or information was taken from published radiographs [Le Peyrat 1 (Patte, 1963); Teshik Tash (Gremyatski and Nesturkh, 1949); Zaskalnaya VI (Kolosov, 1974)]. No attempt was made to assign sex to any of the fossil individuals, as so many were isolated jaw fragments, very few had associated pelvic remains, and sex assignment of immature skeletal remains is fraught with uncertainty. A complete listing of the fossil hominid specimens utilized for this study is given in Table 1.

## METHODS

The methodology for scoring the calcification status of the teeth in the fossil and recent samples is a modification of the system

developed by Demirjian et al. (1973). Five extra stages were added for each tooth type which fall in between the eight original Demirjian stages. The scoring system was also modified to account for the higher frequencies of taurodont molars in the fossil samples (which affects the timing of appearance of the root cleft, one of the scoring criteria in the original Demirjian system). A complete description of this 13 stage scoring system is presented in Tompkins (1996).

Because there are relatively few fossils with reference teeth at the exact same stage of development (reference teeth are those whose calcification stage is held constant across samples when comparing the attained calcification stages of another tooth), a comparative approach was developed which maximizes the use of the fossils as samples. For any tooth comparison each fossil was compared to the appropriate modern human distribution of relative dental development (for example, comparing  $M_2$  development when  $M_1$  is at stage 7) and was assigned a rating of 1 to 5 based on where its relative calcification score fell with regard to the recent human median. If the fossil score was two or more stages below the respective recent human median, it was assigned a 1. If it was at least one stage below, but less than two stages below, it was assigned a 2. If it fell within the range between, but not including, one stage below and one stage above the median, it was assigned a 3. If it was at least one stage above, but less than two stages above the median it was assigned a 4. If it was two or more stages above the median, it was assigned a 5. The categories were defined this way to account for the fact that the median calcification scores for some recent human distributions were fractional numbers, not pure integers.

Scores for the fossil samples as a whole for each tooth comparison ( $M_1$ ,  $M_2$ ,  $M_3$ ,  $P_3$ ,  $I_1$ , and canine) were then derived by summing the individual fossil scores. For example, there were five specimens in the Neandertal/archaic *Homo* group suitable for comparing relative  $M_3$  development to recent humans. The scores assigned to these five specimens were added and this sum represents the sample score for Neandertal/archaic *Homo*  $M_3$ 's. The largest possible sample of fossil specimens was obtained by

TABLE 1. *Fossil hominid specimens utilized*

Early Modern/Upper Paleolithic	Neanderthal/archaic <i>H. sapiens</i>
Abri Pataud 26.236	Chateauf-neuf-sur-Charente 1, 2
Badegoule	Combe-Grenal 1
Bruniquel II	Hortus 2
EM 536, EM 538, EM 541	La Chaise 13, 14
Bruniquel Lafaye 25	La Ferrassie 8
Fontchevade 1957-53	La Quina H18
Grotte des Rois 1955-148-1	Pech de l'Aze
Isturitz III	Roc de Marsal 1
1937: 1950-6, 1950-5-1	Engis 2
La Geniere #3 (1926)	Gibraltar 2
La Madeleine child (#4)	Archi (Reggio Calabria)
Lagerie-Basse 1, 2, 3, 5, 6	Le Fate II
Lagerie-Basse teen	Molare
Le Figuer	Ehringsdorf G
Le Peyrat child	Krapina
Le Placard	#45, #46, #47, #51, #52, #53, #54, #55
56Q29 (68098)	Sipka
DG#31/32 (61401)	Teshik-Tash
Le Roc de Sers 75113 & 11-3	Zaskalnaya VI
Les Fees 1	
Mas d'Azil	Jebel Irhoud 3
Montgaudier 3	Rabat 1 (1972-4)
Rochereil 1945-18	
Saint Germain La Riviere	
1970-8 B3, B4, B5, B6 & 7	
Solutre 1956-49 (671, 1868)	
Magrite 2426, 2678	
(individuals #5, 6)	
Badger Hole 227 31, 226 30	
Mother Grundy's Parlour EN 1.7.1	
Arene Candide VB, VIII, XI	
Baouss-Rousse 1969-9	
Barma Grande 3, 4	
Grotte des Enfants 1, 2	
Paglicci	
Parpall 1	
Brillenhohle 2	
Miesslingtal 22034 (73577)	
Kosdtenski 3, 4	
Mal'ta (older child)	
Vindija 76/232	
Qafzeh 4, 11	
Skhul 1	
Tangiers 1 (Mugharet el'Aliya)	

utilizing data from either jaw and using different reference teeth where necessary (e.g., to maximize the fossil sample size for comparisons of canine development, first molars and both premolars were utilized as reference teeth and a mixture of fossil specimens with either maxillary or mandibular teeth were included). Priority was given to using the mandibular teeth of the fossil hominids for comparison whenever possible as the recent human sample sizes were larger for these than for maxillary teeth. No fossil individual is represented more than once in any single comparison.

The probability of obtaining such a fossil sample score from the recent human sam-

ples was determined using a bootstrap method. A computer program (written for this purpose by Steven Churchill) was utilized to randomly pull repeated samples from the recent humans of the exact same size and configuration as the fossil samples.<sup>1</sup> For example, the Early Modern/Upper Paleolithic M3 sample consisted of six individuals where mandibular teeth were used and one where maxillary teeth were used, with M<sub>2</sub> serving as the reference tooth for the first

<sup>1</sup>The approach developed by Press et al. (1989) for insuring random number generation was utilized for this bootstrap program.

six, while  $M^2$  was used for the seventh. Of the first six individuals, three possessed an  $M_2$  at stage 12, while the  $M_2$ 's of the other three were at stages 5, 9, and 11. The seventh individual's  $M^2$  was at stage 9. The sample of individuals with  $M3$ 's repeatedly pulled from the recent human groups were matched exactly to these reference tooth requirements. For each comparison, 10,000 samples were randomly pulled from the recent human groups to derive a distribution of possible sample scores. The proportion of scores from the smaller tail of the distribution was used as a one-tailed probability of obtaining a sample score as extreme or more extreme than the actual fossil sample score.

In some cases the fossil samples have been compared to the combined recent sample while in other cases they have been compared to various subsets of the recent humans. The latter was done in cases where significant differences were found among the recent human samples or between the sexes within a recent human sample, as noted below. [See Tompkins (1991, 1996) for more information on these recent human differences.] Fossil specimens were utilized only when a minimum of five recent humans at the same reference tooth stage were available for comparison (i.e., for determining the median calcification stage of the recent human distributions).<sup>2</sup> The fossil hominid sample sizes used for comparing canine development differ in the comparisons to French-Canadian females versus the comparisons to southern African females because some of the French-Canadian sample sizes fell below this minimum.

## RESULTS

Figures 1–6 show the distribution of the hominid samples about the median calcifica-

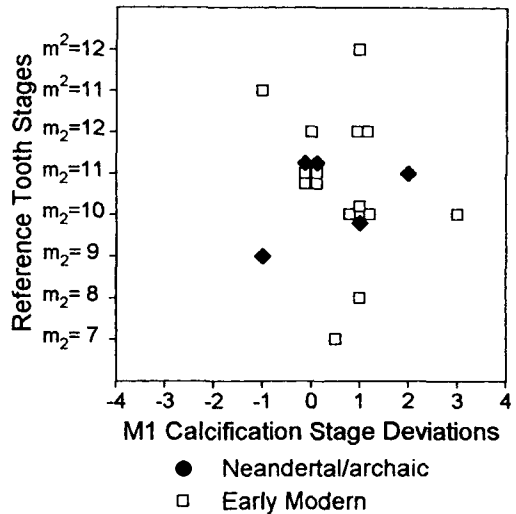


Fig. 1. Deviations of fossil hominid  $M1$ 's from median calcification stages of Native Americans, using deciduous  $m_2$  as the reference tooth. Note the pattern of advancement in the Early Modern/Upper Paleolithic sample.

tion stages of the recent human samples at the various reference tooth stages. The bootstrapped  $P$ -values for all fossil hominid-recent human comparisons are presented in Table 2. Fossil hominid sample sizes are shown next to each  $P$ -value. The following is a detailed summary of the fossil hominid-recent human comparisons:

1. For the  $M1$  comparisons  $dm_2$  was used as the reference tooth. The only recent human group containing individuals with  $dm_2$  still developing, and thus the only recent human group which could be used for  $M1$  comparisons, was the Native Americans. The Early Moderns are advanced over the Native Americans in  $M1$  development while the Neandertal/archaic *Homo* group is not. The advancement of the Early Moderns compared to the Native Americans can be seen in Figure 1. For the  $M1$  comparisons the Neandertal/archaic *Homo* sample size is one-third that of the Early Moderns, while in all other comparisons it is at least 50% of the Early Modern sample size. A larger sample of Neandertal/archaic *Homo* specimens might possibly show them to be advanced over Native Americans as well.

<sup>2</sup>The recent human sample sizes utilized for comparing fossil hominids at specific stages of reference tooth development ranged from a minimum of 5 to a maximum of 200. The average size of the recent human samples at various reference tooth stages used to determine the probabilities given in Table 2 ranged from 23.2 to 86.0 for the various tooth comparisons, with a mean of 53.4. The fact that all bootstrapped score distributions roughly approximated bell-shaped distributions and that some bootstrapped sample scores were generated in frequencies as low as 0.0001 (1/10,000) shows that these sample sizes were sufficient for the purpose of this bootstrapping procedure.

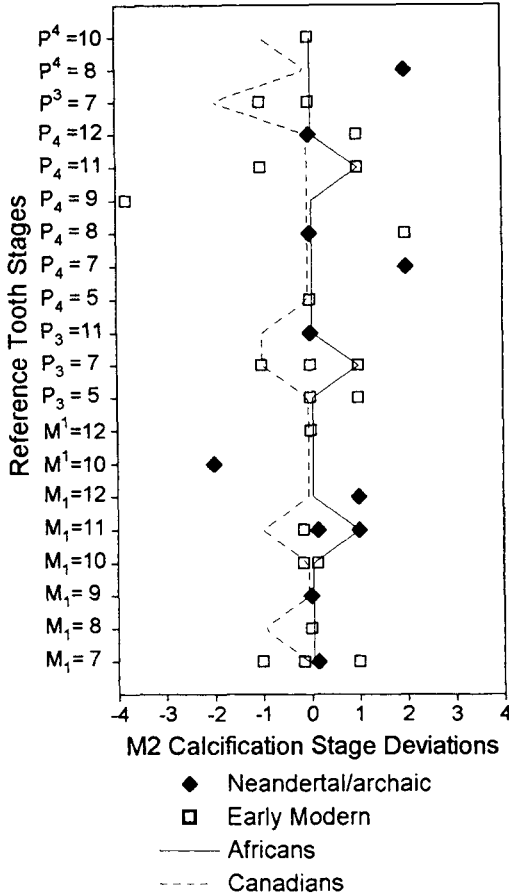


Fig. 2. Deviations of fossil hominid M2's from median calcification stages of combined recent human sample, using M1, P3, and P4 as the reference teeth. Deviations of southern African and French-Canadian medians from combined recent human sample indicated by solid and dashed lines. Both fossil samples are advanced over French-Canadians, but not southern Africans.

2. M1, P3, and P4 were used as reference teeth for the M2 comparisons. The hominid samples were compared to French-Canadians and southern Africans separately because the latter are somewhat advanced over the former in their relative M2 development (see Tompkins, 1991, 1996). Both fossil groups are advanced over French-Canadians in relative M2 development. However, neither fossil group differs significantly from the southern Africans. Figure 2 shows the distribution of the two fossil samples about the combined recent human medians and

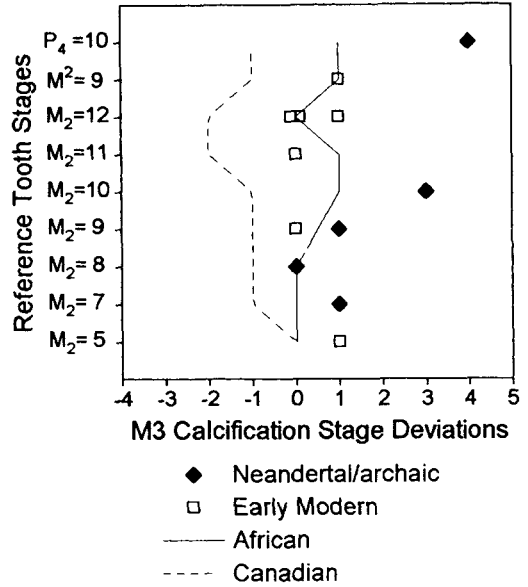


Fig. 3. Deviations of fossil hominid M3's from median calcification stages of combined recent human sample, using M2 and P4 as the reference teeth. Deviations of southern African and French-Canadian medians from combined recent human sample indicated by solid and dashed lines. Note the distinct separation between the French-Canadian and southern Africans medians. Both fossil samples are highly advanced over French-Canadians. Only the Neandertal/archaic *Homo* sample is advanced over southern Africans. The great advancement of Rabat 1 (individual at top right) is most likely due to use of its unusually delayed P<sub>4</sub> as the reference tooth (see text).

also shows the deviations of the African and French-Canadian samples' medians from the combined recent human medians.

3. For the M3 comparisons, M2 and P4 were used as reference teeth. The hominid samples were compared to French-Canadians and southern Africans separately because the latter are highly advanced over the former in M3 calcification. Both fossil groups have relative M3 development greatly advanced over French-Canadians. When compared to southern Africans only the Neandertal/archaic *Homo* group is advanced. However, this advancement is due mainly to the inclusion of the Rabat 1 specimen in the sample. In this fossil specimen the still-developing P<sub>4</sub> was used as the reference tooth as M<sub>1</sub>, M<sub>2</sub>, and P<sub>3</sub> have all completed their root development. Given that

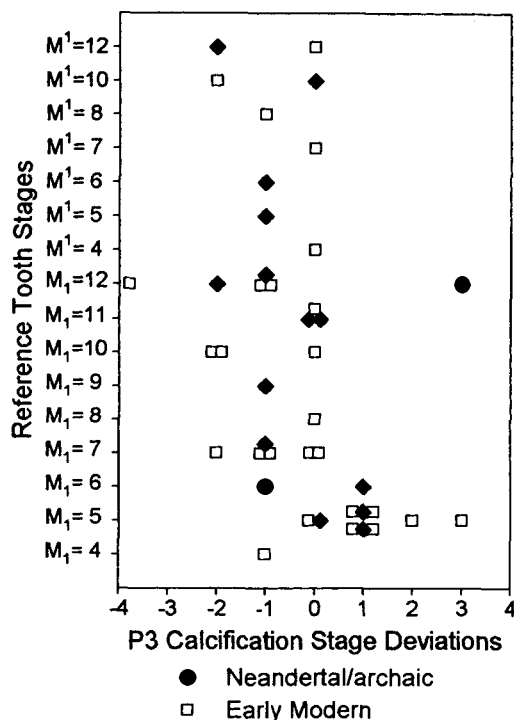


Fig. 4. Deviations of fossil hominid P3's from median calcification stages of combined recent human sample, using M1 as the reference tooth. Both fossil samples appear delayed.

the Rabat specimen's  $P_3$  and  $M_2$  development are completed and the lower canine is very near completion, while  $P_4$  is still several stages from completion, it seems likely that its  $P_4$  is at the delayed end of the range of  $P_4$  variability. Thus its  $M_3$  looks more advanced than it probably would if it were possible to compare it earlier in its development using  $M_2$  as the reference tooth. When Rabat 1 is excluded from the Neandertal/archaic *Homo* sample the  $P$ -value rises to 0.1254. Nonetheless, this is still somewhat low for such a small sample size ( $n = 4$ ) and three of these fossil specimens fall above the southern African medians.<sup>3</sup> This suggests that if a larger sample of Neandertal/archaic *Homo* specimens was available it might prove to be ad-

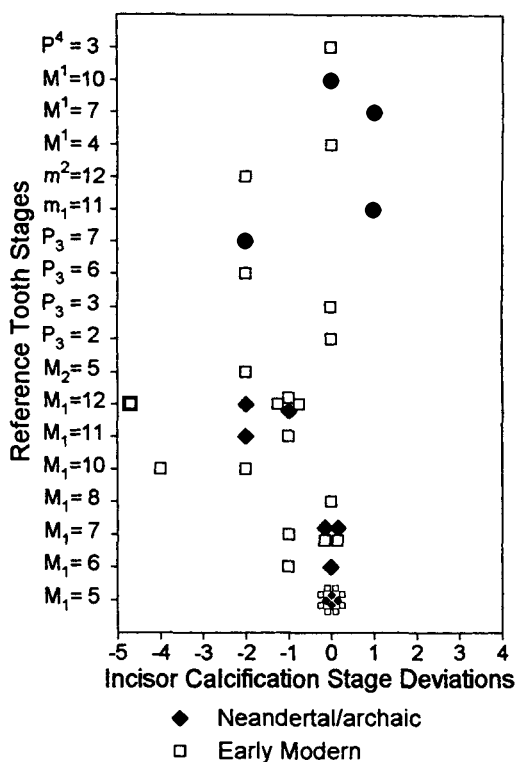


Fig. 5. Deviations of fossil hominid I1's from median calcification stages of combined recent human sample, using M1, M2, deciduous m1 and m2, and P3 and P4 as the reference teeth. Both fossil samples are delayed, especially the Early Modern/Upper Paleolithic sample, which contains no individuals falling above the recent human medians.

vanced over the southern Africans, even without the inclusion of Rabat 1. Figure 3 gives a clear indication of the magnitude of differences between the fossil samples, the combined recent human medians, and the French-Canadian and southern African medians. The difference between the latter two recent human samples is clearly evident in the degree of separation of their respective medians, as is the marked advancement of both fossil hominid samples over the French-Canadians.

4. With regard to the comparisons of P3 development, although the  $P$ -values for both fossil hominid groups are somewhat higher than 0.05, they are low enough to indicate that both fossil groups are delayed in their P3 development relative to the M1. The dis-

<sup>3</sup>With Rabat 1 removed, the probability of drawing the Neandertal/archaic *Homo* sample from the French-Canadians is  $P = 0.0012$  ( $n = 4$ ).

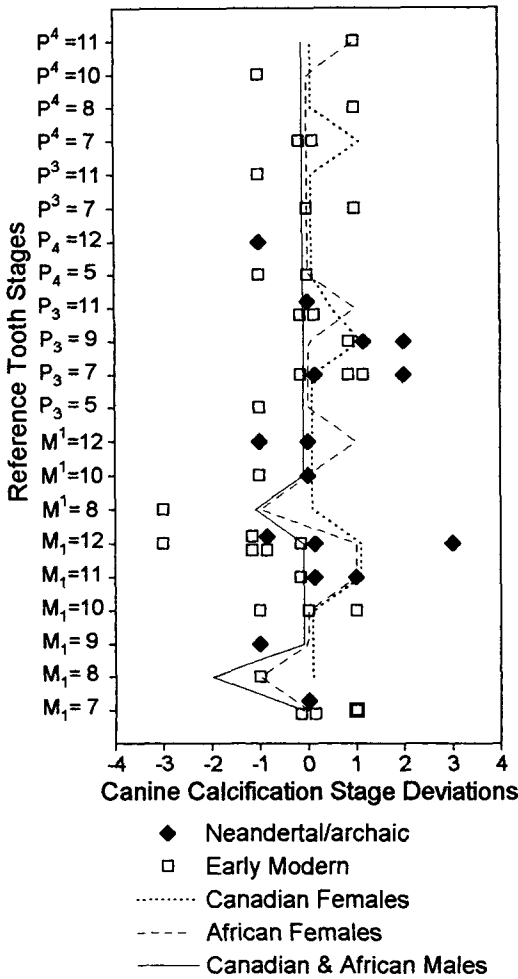


Fig. 6. Deviations of fossil hominid canines from median calcification stages of combined southern African and French-Canadian samples, both males and females, using M1, P3, and P4 as the reference teeth. Deviations of medians of combined African and Canadian males, African females, and French-Canadian females indicated by the various lines. Although the patterns are complex, the Early Modern/Upper Paleolithic sample is delayed compared to both French-Canadian and southern African females, but not compared to the recent human males. The Neandertal/archaic *Homo* sample does not differ from the two female samples, but appears advanced over the recent human males.

tribution of the fossil samples about the combined recent human medians in Figure 4 supports this conclusion; there are clearly more fossils falling below the recent human medians than above them.

5. For I1 comparisons, M1, M2, P3, P4,

dm1, and dm2 were used as reference teeth. The Early Modern group is highly significantly delayed in relative incisor development, whether compared to the combined recent humans or solely to the Native Americans (who may be somewhat delayed compared to the other two recent groups; see Tompkins, 1991, n.d.). The Neandertal/archaic *Homo* group is also delayed in their incisor development, although the *P*-value for the comparison to Native Americans is somewhat over the 0.05 significance level. Figure 5 clearly shows the delayed patterning of the Early Moderns, and to a lesser extent the Neandertal/archaic *Homo* group, relative to the combined recent human medians.

6. For canine comparisons, the fossil hominids were compared to males and females of the southern African and French-Canadian samples separately because sex differences in canine calcification were found in these recent humans (see Tompkins, 1991, 1996). (These two recent human groups were the only ones in which the sex of each individual was known.) It is expected that similar differences characterize the fossil hominid groups. Unfortunately the unknown proportion of sexes in the fossil hominid samples renders comparisons of canine development of limited use. The fossil hominids were compared to the African and French-Canadian females separately because the former group is delayed in canine calcification compared to the latter, whereas no such difference exists between the males of these two groups. For these canine comparisons M1, P3, and P4 were used as the reference teeth.

The Early Modern sample is highly significantly delayed in relative canine development compared to southern African or French-Canadian females, but not compared to the males of these two groups. The Neandertal/archaic *Homo* sample does not differ from either of the recent female groups but they appear to be somewhat advanced over the recent human males, although the *P*-value is somewhat higher than 0.05. Figure 6 shows the deviations of the fossil hominid groups from the combined recent human sample medians and also the deviations of the medians of the combined African and



TABLE 2. One-tailed bootstrapped probabilities of drawing fossil hominid samples of relative dental development from recent human samples

Tooth—Human group used for comparison	Early Modern/Upper Paleolithic			Neandertal/archaic <i>Homo</i>		
	<i>P</i>	Direction <sup>1</sup>	<i>N</i>	<i>P</i>	Direction <sup>1</sup>	<i>N</i>
M1—Native American	0.0101	+	15	0.3862	+	5
M2—Canadians	0.0155	+	22	0.0111	+	11
M2—Africans	0.2457	—	22	0.3507	+	11
M3—Canadians	0.0000	+	7	0.0000	+	5 <sup>2</sup>
M3—Africans	0.4428	+	7	0.0531	+	5 <sup>3</sup>
P3—Combined <sup>4</sup>	0.0590	—	26	0.0659	—	16
I1—Combined <sup>4</sup>	0.0000	—	27	0.0176	—	14
I1—Native American	0.0000	—	27	0.0789	—	14
C—Canadian ♀	0.0000	—	26	0.3582	—	13
C—African ♀	0.0000	—	29	0.2350	—	15
C—Canadian and African ♂	0.3678	—	32	0.0820	+	16

<sup>1</sup>Symbols denote whether fossil sample score fell above (+) or below (—) mean of bootstrapped scores. Probabilities are from smaller tail of bootstrapped distribution.

<sup>2</sup>With Rabat 1 removed,  $P = 0.0012$  ( $n = 4$ ). See text.

<sup>3</sup>With Rabat 1 removed,  $P = 0.1254$  ( $n = 4$ ). See text.

<sup>4</sup>Combined recent human groups, both males and females, used for comparison.

French-Canadian male sample and the African female and French-Canadian female samples from the combined recent human medians.

## DISCUSSION

Two general hypotheses regarding the significance of recent human population variability in relative dental development, in particular relative M3 and M2 development, have been articulated in Tompkins (1993, 1996). These hypotheses will be briefly discussed below and their implications for similarities and differences between the fossil hominids and recent human will be considered.

The first hypothesis proposes that an interplay between tooth and jaw sizes determines the relative and absolute timing of dental calcification and eruption (Bradley 1961; Brown, 1978; Fanning, 1962; Hunt, 1959; Moorrees, 1967; Odusanya and Abayomi, 1991; Stringer et al., 1990) and also the frequency of third molar agenesis (Anderson et al., 1975). Stated simply, populations characterized by jaws with more space for successively developing teeth should have advanced calcification and eruption schedules, especially for second and third molars (both relatively and absolutely), and lower frequencies of third molar agenesis compared to populations with greater space re-

strictions.<sup>4</sup> Thus the earlier relative M3 and M3 calcification found in the fossil groups and southern Africans could be due simply to tooth/jaw size relationships. Upper Pleistocene hominids and southern Africans may have more space in their jaws for their developing molars than do French-Canadians and other European-derived populations, and this may lead to an advancement in their relative molar development. Neandertals certainly had sufficient space for their third molars, given their characteristic retromolar spaces. The Early Moderns may also have

<sup>4</sup>Anderson et al. (1975) found that individuals with M3 agenesis also have shorter maxillary lengths. Chagula (1960) reports that only 1.9% of East African males have agenesis of any of their third molars, a figure lower than that known for Europeans/European Americans and Eskimos (Fanning, 1962). However, Merz et al. (1991) have found that while African Americans have less crowded teeth than European Americans, the mesio-distal diameters of their mandibular canines, premolars, and first molars are larger than in European Americans. They did not measure the diameters of second and third molars, but it is possible that these teeth are also larger than in European Americans. Thus it may be that relative molar development patterns and the frequency of third molar agenesis are due to a combination of two more or less independently varying factors: tooth size and jaw size.

Garn et al. (1961, 1963) found that M3 agenesis was correlated with delayed calcification of other postcanine teeth. They suggest that agenesis may be one end of a range in the expression of genetic factors responsible for delayed tooth formation. As agenesis can be considered the extreme of tooth size reduction, it is possible that population differences in just a few gene loci simultaneously affect the timing of molar development, molar size, and M3 agenesis.

achieved greater space for these teeth, but by different means than the Neandertals (see Merz et al., 1991, for a discussion of the various means of increasing space for teeth).

The second hypothesis postulates that human population variability in relative molar development reflects differences in the *potential* rapidity (or slowness) of skeletal maturation between human populations. It is based on reports of advanced skeletal and dental development in several African and African-derived populations (Chagula, 1960; Fanning, 1962; Garn et al., 1972; Hassanali, 1985; Hiernaux, 1968; Malina and Little, 1981; Marshall et al., 1970; Massé and Hunt, 1963; Odusanya and Abayomi, 1991; Owen et al., 1974; Roche et al., 1975; Tanner, 1962) and ideas presented in Chagula (1960), Eveleth and Tanner (1976), and Fanning and Moorrees (1969). This hypothesis proposes that there are differences between populations in genes operating during infancy and childhood which affect the timing (both relative and absolute) of beginning dental and skeletal formation. Because skeletal development is more plastic than dental development, populations with advanced formation of their M3's and M2's and various skeletal elements may not maintain their advanced skeletal development throughout childhood and the adolescent years compared to populations with relatively delayed M3 and M2 development. Indeed, some populations with the potential for relatively advanced skeletal development may even become retarded in skeletal development (as is often found in African and African-derived populations [Levine, 1972; Michaut et al., 1972; Tobias, 1958]). However, the smaller amount of plasticity in dental development means that populations with advanced relative molar development will maintain this advancement throughout their growth period.

There are several studies showing that various African groups are advanced over Europeans in third molar eruption (Chagula, 1960; Fanning, 1962; Hassanali, 1985; Odusanya and Abayomi, 1991; Suk, 1919). This advanced M3 eruption and the advancement of southern Africans over French-Canadians in relative M3 calcification appear to be due largely to earlier initial

formation of this tooth (see Tompkins, 1996). Although further studies on the actual chronology of tooth formation in African populations are needed to confirm this conclusion, it is in full accord with a recent study of incremental markings in the dentine and enamel of an unidentified black male of probable West African origin by Dean et al. (1993b). This latter study indicates that initial formation of the mandibular third molars in this black male began around 6.4 years, an age which is much earlier than in most Europeans and European Americans. While this individual probably falls at the extremely advanced end of the range of variation in African M3 formation, his example nonetheless suggests that significant differences exist between at least some African and European populations in the initiation of M3 development. Thus it is not unreasonable to hypothesize that population differences in skeletal maturation and relative M3 and M2 development are causally related to population differences in pleiotropic genes acting on both hard tissue systems during childhood.

Brain weight and body size account for most of the variability between primate genera in many life history parameters (Harvey and Clutton-Brock, 1985; Harvey et al., 1986), and may well be the two most important physiological factors determining life history patterns and overall rates of ontogeny. Given that Upper Pleistocene hominids and living humans share very similar body weights and brain sizes, we would expect these groups to share fairly similar ranges of developmental rates. If one then considers the close taxonomic affinity between these groups,<sup>5</sup> it is reasonable to assume that Upper Pleistocene hominids were characterized by developmental pathways and hormonal control systems for rates of dental and skeletal development very similar to those of living humans. Thus, extrapolating the probable significance of variability in relative molar development for potential

<sup>5</sup>Upper Paleolithic specimens are considered *H. sapiens* in the biological species sense; Neandertals and "archaic" *H. sapiens* may actually differ at the species level from modern humans, but are still very closely related to living humans.

rate of skeletal maturation from living humans to Upper Pleistocene hominids is reasonably justified.

Assuming that the southern Africans' advancement of relative M3 and M2 calcification compared to French-Canadians (and by extension, Europeans and Euroamericans in general) is an indicator of their potential for relatively precocious skeletal development, then the similarities between both fossil groups and southern Africans in advanced relative M2 and especially M3 development suggests that the fossil groups possessed comparable potentials for advanced skeletal maturation compared to French-Canadians (and other European-derived populations). It is therefore not surprising that Heim (1982) found some possible indications of precocious skeletal development in the immature Neandertal remains from La Ferrassie, relative to his small comparative samples of European children. Such differences from "modern humans" might not have been found had he been able to compare the La Ferrassie children to sufficiently large samples of modern Africans or other populations.

The results of this study indicate that relative M3 development in the Neandertal/archaic *Homo* group is advanced not only compared to French-Canadians but also compared to southern Africans. As discussed above, this result is mainly due to the inclusion of Rabat 1 in the sample. With Rabat 1 excluded, the remaining sample of four Neandertals does not differ from the southern Africans, although the *P*-value of 0.1254 for this comparison is still somewhat low for such a small sample. Only a larger fossil sample would be able to confirm whether or not Neandertals and archaic *H. sapiens* actually possessed accelerated M3 development compared to southern Africans. If Neandertals and archaic *H. sapiens* did indeed have M3 development which was advanced over southern Africans, one might argue that they possessed the potential for somewhat advanced skeletal maturation compared to southern Africans.

These two general hypotheses concerning the significance of population variability in relative dental development (especially relative M3 and M2 development) are not necessarily mutually exclusive. Both tooth/

jaw size relationships and genetically based population variability in the tempo of dental and skeletal development may be factors in the different patterns of relative dental development found between the recent human and fossil hominid samples discussed here. However, for the sake of generating alternate hypotheses which are potentially testable using recent human and fossil hominid skeletal material and appropriate data from studies of living humans, it is probably best to consider them as mutually exclusive.

Regardless of the significance of advanced M2 and M3 calcification for other somatic systems, the fact that both fossil groups share relatively advanced M3 calcification with Africans, who are noted for earlier ages of M3 eruption than in Europeans and European Americans (Chagula, 1960; Fanning, 1962; Hassanali, 1985), supports Wolpoff's (1979) hypothesis that the Krapina Neandertals erupted their third molars earlier than the approximately 20 years common for European Americans. While the mean age of M3 eruption in Neandertals (or Early Moderns) may not be as early as the 15 years suggested by Wolpoff, it is very likely that it was significantly earlier than the norm for European Americans. However, this same advancement would have also characterized the Early Modern sample.

While the fossil hominids' relative molar development patterns are essentially matched by those of southern Africans, there are other differences between the fossil hominids and recent humans which could not be matched by any of the three recent human groups. Whether or not these latter differences indicate some deviation from recent human ontogenetic patterns is debatable.

The apparent advancement of the Early Modern's M1 development suggests the possibility of accelerated development in other systems during early childhood. However, relative M1 calcification of the fossil hominids could only be compared to Native Americans. It is possible that the Early Moderns would not look advanced compared to Africans or some other population. Similar data on children of equivalent developmental stages from African and other populations is necessary in order to confirm or

refute this apparent advancement of M1 in Early Moderns.

The significance of the canine differences found between the fossil hominids and recent human is difficult to assess due to the unknown sex composition of the fossil samples. It is possible that there is a much greater proportion of males in the Early Modern group, which would account for this sample's delay compared to the recent females but not the males. It is also possible that the Neandertal/archaic *Homo* sample has a high proportion of females which would account for their advancement compared to the recent males and the lack of difference from the recent females.

The other comparisons where the fossils' patterning cannot be clearly matched by any of the recent human subgroups are those of the central incisor and first premolar, both of which are delayed in their relative development in the fossil samples. At present, the significance (if any) of these delays in both hominid groups is unclear.

Perhaps the delayed relative calcification of the Neandertal/archaic *Homo* incisors and premolars is a reflection of their larger size compared to most recent humans (Trinkaus, 1983; Wolpoff, 1971). The larger size of these teeth may have required more time for completion of development and/or calcification. Yet such an explanation could not be applied to the delayed incisor and premolar development seen in the Early Modern group, as they are characterized by incisor and premolar sizes comparable to recent humans (Trinkaus, 1983; Wolpoff, 1971).

The same inconsistency applies if one argues that the reduction in incisor and premolar size across the Middle-Upper Paleolithic transition was associated with delayed development of the permanent incisors. While this might explain the delayed development of these teeth in the Early Modern group, it could not be logically applied to the Neandertal/archaic *Homo* group.

One other possibility exists regarding this incisor and premolar delay in the fossil groups. It may be that both hominid samples are characterized by advanced development of their M1's compared to recent humans, while the actual chronological maturation of their incisors and premolars

was very similar to modern humans. Such a condition would produce the pattern of delayed relative incisor and premolar calcification found in this study, and would be in accord with the advancement of M1 development (relative to dm2) found in the Early Modern sample. Without data on absolute chronological timing of tooth formation, this remains a very speculative suggestion.

It is of interest to note that this delay in incisor and first premolar development relative to the first molar is similar to the pattern found when apes are compared to modern humans (Smith, 1992, Figure 5), although it is undoubtedly less exaggerated. It is thus possible that delayed relative incisor and first premolar calcification is the plesiomorphic condition for hominoids.

This study has shown that both hominid samples share essentially similar patterns of relative dental development. Both hominid groups also possessed adult brain and body sizes essentially similar to those of modern humans. These combined observations support the idea that no significant differences existed between the hominid samples in their overall ontogenetic rates (i.e., the length of their growth periods), nor between either hominid group and modern humans. Thus it appears that the extended growth period characteristic of modern humans had evolved by the Upper Pleistocene. However, the data presented here is by no means sufficient to prove the validity of these latter conclusions. Much work remains to be done on histological markers of tooth formation in Upper Pleistocene hominids (Dean et al., 1986; Stringer et al., 1990) and variability in the periodicity of enamel (and dentine) microstructures between human populations (Mann et al., 1993) and hominoid species. These types of studies will be necessary in order to more confidently assess the nature of ontogenetic patterns in fossil hominids.

## CONCLUSIONS

Comparisons of relative dental development between recent humans and Neandertal/archaic *Homo* and Early Modern/Upper Paleolithic hominids show that the fossil

hominid groups do differ from some recent human populations. M2 and especially M3 development in both hominid samples is significantly advanced over that of French-Canadians, but is matched by that of southern Africans (with the possible exception of the Neandertal/archaic *Homo* group). Based on hypotheses presented here and in Tompkins (1993, 1996), the similarity in advancement of M3 development between both fossil groups and the southern Africans compared to French-Canadians (and probably most other European/Euroamerican populations) suggests that the fossil hominids and southern Africans are characterized by similar potentials for more precocious skeletal maturation than in French-Canadians (and other European/Euroamerican populations). Alternatively, the similarities in relative M3 and M2 development between southern Africans and both fossil hominid groups may be the result of tooth/jaw size relationships. These hypotheses are potentially testable with fossil hominid and recent human skeletal samples and data from living humans.

Aside from those cases where comparisons are necessarily limited to only one of the recent humans samples (M1 development), or where unknown sex composition in the samples is a confounding factor (canine development), there are two comparisons where both fossil groups are delayed relative to all the recent human samples: central incisor and first premolar development. The significance of these latter differences is unclear at present.

It thus appears that hominid dental development patterns have continued to evolve from the Lower Pleistocene (Bromage, 1987; Conroy and Vannier, 1987, 1991; Smith, 1992) on through the later Pleistocene up to the Holocene. The significance of differences in various aspects of dental development between apes, fossil hominids, and recent humans for ontogeny and life history patterns continues to be debated. Nonetheless, studies of these hard tissue developmental patterns hold significant promise for our understanding of the ontogenetic changes which occurred during hominid evolution, changes which undoubtedly have important behavioral implications as well.

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